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SYNOPSIS OF RECENT PROGRESS IN THE STUDY OF GRAPTOLITES.

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THE graptolites have been a puzzling group of fossils to palæontologists ever since they were discovered. Though on account of their excessive abundance in certain strata, the beauty and variety of their delicate forms, and the strange mode of their vertical and horizontal distribution they have always received a full share of attention, the knowledge of their morphology has made only little progress, owing to their preservation as completely flattened carbonaceous films. As a result of this incomplete knowledge of their structure, the systematic conscience of palæontologists acquiesced in their being assigned to the Hydrozoa, in spite of the difficulty arising from the formerly commonly accepted presence of the virgula or "solid rod" in the rhabdosome and the supposed floating habit of the graptolites. The fact that they were found to furnish excellent data for the detailed division into zones of the Cambrian, Ordovician, and Silurian strata prevented their neglect, although so refractory to all attempts at close morphologic investigation, and the search for them in the field never relaxed. The gratifying result of this persistency is that at last material has been found which is accessible to modern refined preparative methods and to microscopic analysis.

Gümbel ('78) was the first to isolate stipes imbedded in limestone. Later Törnquist ('90, '92) obtained much valuable information by grinding pyritized material. The best results, however, have been obtained by the methods employed lately by Holm ('90, '95) and Wiman ('93, '95). For the details of these preparative methods, the reader is referred to Wiman's interesting account in his paper, "Ueber die Graptoliten" ('95), the review ('96) of his work in the *American Geologist*, and to Wiman's "Structure of the Graptolites" ('96).

Both Holm and Wiman isolated stipes by dissolving the matrix. Various acids have been used for dissolving, according to the nature of the rock. Limestone material was found the simplest to handle, and muriatic acid in different states of solution or milder solvents, such as acetic acid, gave good results. Especially interesting to American readers is the description which Wiman gives of his treatment of highly aluminous clay slates, as these are almost the only graptolite-bearing rocks found here. Wiman subjected them to the successive action of acetic and hydrofluoric acids. J. M. Clarke handled similar material successfully with acids and caustic potash. These methods, however, fail with a matrix that does not contain a sufficient lime-content to lose its consistence by the dissolution of the latter, and this appears to be the case with most of the American graptolite-bearing rocks. Wiman had also occasion to isolate graptolites from chert-masses by successively subjecting the rock to a treatment with concentrated hydrofluoric acid and muriatic acid.

The isolated graptolites have been decolored both by Holm and Wiman in different ways. Wiman used first Schultze's maceration medium, which is a solution of calcium chlorate in nitric acid, but later substituted for it eau de Javelle or potassium hypochlorite, because Schultze's medium is often too harsh. The specimens were then cleared with chloroform or other clearing fluids and mounted in Canada balsam, or, where this method could not be used on account of the thickness of the periderm, the specimens were prepared for the microtome according to the methods used by zoologists.

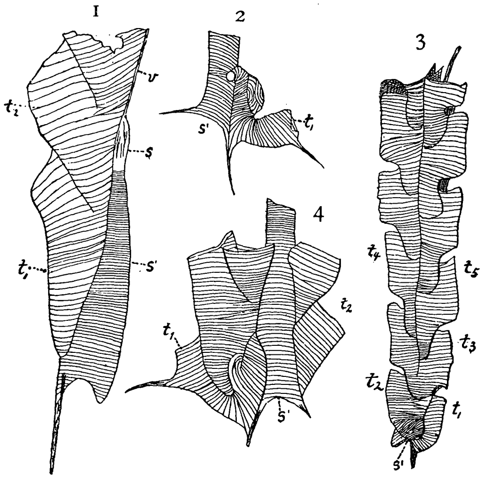
By the application of these preparative methods histological and morphological discoveries have been made.

The histology of the graptolites has been especially advanced by the researches of Holm (**'90**), Sollas (**'94**), and Perner (**'94**). The last two investigators demonstrated the presence of three different layers in the periderm of Monograptus; *viz.*, a stronger middle layer between two thinner ones. Wiman (**'95**) verified Perner's observations as to *Monograptus priodon* and discerned the two outer layers in Diplograptus. The middle layer in Diplograptus contains the growth-lines observed repeatedly before. The histology of the Retioloidea has been studied by the above-named geologists and by Tullberg (**'82**) and Törnquist (**'90**, **'93**). Holm found three layers; *viz.*, smooth epidermic and endermic layers, which inclose the latticed network of chitinous threads, from which this group derives its name.

In the Dendroidea Wiman (**'95**) observed the two outer layers.

However interesting the discovery of the differentiation of the periderm of the graptolites is, especially on account of its bearing on the question as to the zoological affinities of this group, it is surpassed in importance by the knowledge which has been obtained as to the morphology and development of the graptolites. In reviewing the progress made in these directions we will separately regard the Graptoloidea, Retioloidea, and Dendroidea.

As an understanding of the conformation of the rhabdosome rests with the knowledge of its growth from the sicula, it will be opportune to review first the fundamental results obtained by Wiman as to the growth of the initial part of the rhabdosomes of Monograptus (**'93**), Diplograptus (**'93**), and some other Graptoloidea. The sicula of these consists of a thin-walled "initial part," which is prolonged into a process, the "virgula," and of the "apertural part," which shows distinct growth-lines and a three-spined symmetrical aperture (Fig. 1, *s*). From the sicula sprouts a new individual, the first theca (Holm considers the apertural part of the sicula already as "first theca"), which in Monograptus lies alongside the sicula and grows at once in an opposite direction (Fig. 1, *t*). From this theca grows another. The continuation of this process and the arranging of the thecæ in one series along the virgula produces the monoprionidian rhabdosome of Monograptus. Also from the sicula of Diplograptus, as Törnquist ('93) and Wiman found almost simultaneously, there sprouts but one bud, and Diplograptus is, therefore, also monoprionidian. The first theca, however, grows at first towards the aperture of the sicula and then bends in the same direction as the thecæ in Monograptus (Figs. 2, 3). The thecæ are arranged in two series, thus producing the diprionidian aspect. The supposition that the diprionidian graptolites consist of two coalescing monoprionidian branches, the double virgula and the double longitudinal septum of the older descriptions, has thus been refuted; the observations of Tullberg, Törnquist, and Wiman prove that not even a single longitudinal septum is always present, and that, if one is present, it does not necessarily extend throughout the entire length of the rhabdosome. Fig. 4, representing a rhabdosome of Climacograptus,



In Figs. 1-8, s = initial part of sicula; s_1 = apertural part of sicula; v = virgula; t = theca.

FIG. 1. — *Monograptus dubius* Suess : sicula end from sicula side (Wiman).
FIG. 2. — *Diplograptus sp.* : sicula end from sicula side (Wiman).
FIG. 3. — The same : a later stage from anti-sicula side (Wiman).
FIG. 4. — *Climacograptus kuckersianus* Holm : sicula side (Wiman).

demonstrates that a septum is formed, where the thecæ, instead of sprouting on the opposite side of the adjacent older thecæ (t_1 t_2), spring from the same side as the latter did (t_4 t_5).

Holm ('95) obtained most valuable information on the internal structure and development of some other important genera of the Graptoloidea; *viz.*, of Didymograptus, Tetragraptus, and Phyllograptus. The most interesting result of his researches is the demonstration of the conformity in the first stages of development of the rhabdosomes in these genera and the Diplograptidæ. It is probable, therefore, that the earlier development of all Graptoloidea was the same, and that it consisted in the formation of only one bud on one side of the sicula.

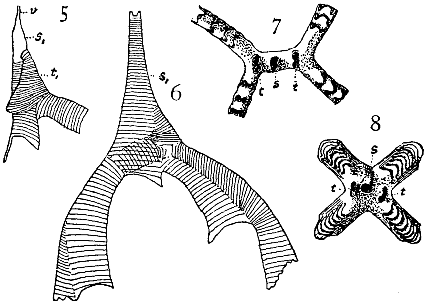


FIG. 5. — *Dichograptid*: anti-sicula side (Wiman).

FIG. 6. — *Didymograptus minutus* Törnquist: anti-sicula side (Holm).

FIG. 7. — *Tetragraptus Bigsbyi* Hall: from the proximal end, with the sicula turned upwards, showing the aperture of the sicula, left and right thecæ, and the thecæ of the four branches (Holm).

FIG. 8. — *Phyllograptus angustifolius* Hall: from the proximal end, with the sicula side turned upwards, showing in the middle the aperture and the oblique position of the sicula, on each side of this the apertures of the left and right thecæ (Holm).

Fig. 5 (from Wiman, '95) shows the initial part of a Dichograptid, and Fig. 6 (from Holm) of *Didymograptus minutus*. Both figures serve to illustrate the diverging growth of the first two thecæ, which produces the characteristic bifurcation of these forms. The repetition of this process (Fig. 7) in Tetragraptus leads to the formation of four branches. The same takes place in the development of Phyllograptus (Fig. 8), "only that the four branches are disposed near each other and form a single, cruciform, four-winged, longitudinal septum."

The conformity of the rhabdosomes of all Graptoloidea has been made probable by these investigations (the Leptograptidæ and Dicranograptidæ have not yet been isolated). The morphology of the entire colonial stock, however, is, owing to the frequent occurrence of only detached rhabdosomes, still little known. Hall ('65) first described stellate groups of Dichograptidæ from Canada; Hermann ('85) such from Scandinavian rocks; Moberg ('93) published a description of a Monograptus with disk; and Gurley ('96) figured a Climacograptus with a disk-like expansion of the virgula. Ruedemann ('95, '97) discovered colonies of two species of Diplograptus in Utica shale which have been deposited under such conditions of quietude as to retain not only all the chitinous appendages of the mature colonies, but also the successive growth-stages of the compound colonies.

It appears from the material that the rhabdosomes of Diplograptus formed umbrella-shaped colonies, consisting of rhabdosomes of various length, which radiate from a central organ, the central disk (Fig. 9). The latter, in its turn, is connected with a larger organ, the basal cyst, that probably served to secure the stability of the colony in the ooze of its habitat. The central disk is surrounded by a cycle of vesicles which

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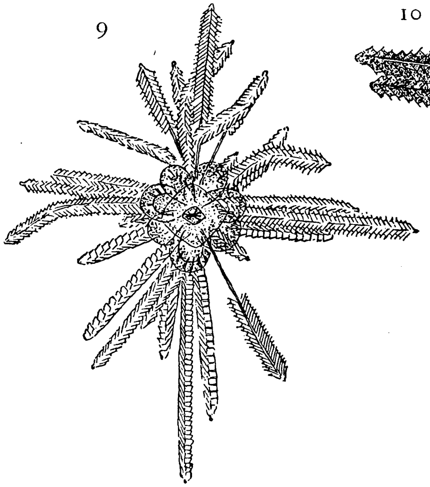

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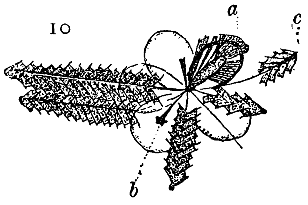
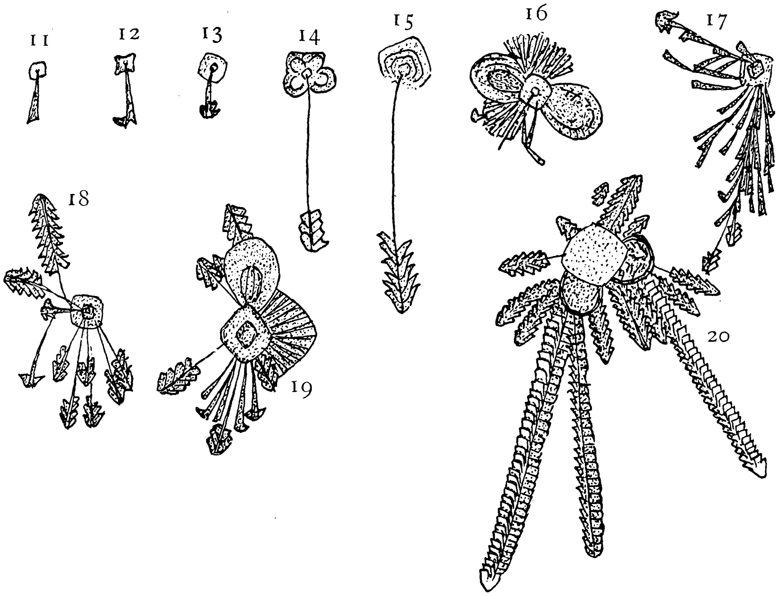


FIG. 9. — *Diplograptus foliaceus* Murch (*D. pristis* Hall): complete colony (Ruedemann).
FIG. 10. — The same: *a*, Gonangium filled with siculæ; *b*, sicula developing into a stipe (Ruedemann).

contain numerous siculæ attached by their apical ends (Fig. 10). The writer compared these vesicles with the gonangia of the sertularians, considering the siculæ as the original chitinous coverings of the embryos. (Holm sees in the initial part of the siculæ the covering of the zooid germ.) The development of the colony is as follows:



Figs. 11–20. — The same: development of a colony (Ruedemann)

1. The sicula is provided with a basal appendage to which it is attached by means of a little round node (Fig. 11).

2. The node becomes a central disk and funicle. The sicula produces at first one theca, then a second, a third, etc., as demonstrated also by Törnquist and Wiman (Figs. 12, 13).

3. The budding of the thecæ along the lengthening hydrocaulus produces the primary rhabdosomes (Figs. 14, 15).

4. While the latter is formed, gonangia, usually as four small capsules, arise from the central disk. At last the latter mature and open. Many, or perhaps all, of the siculæ remain connected to the parent colony (Figs. 16, 17).

5. These siculæ grow out to rhabdosomes (Fig. 18).

6. After this first generation of rhabdosomes has reached a certain age a second generation of gonangia begins to grow (Fig. 19).

7. The siculæ formed in these develop into a new verticil of rhabdosomes.

The result of this mode of development is a colony which consists of different generations of rhabdosomes, recognizable by the different lengths of the latter (Fig. 20). An especially remarkable feature of the colonies is the position of the sicula at the distal end of the rhabdosome in regard to the central disk. The explanation of this peculiar position of the sicula is found in the observation that the first theca turns away from the aperture of the sicula and grows towards the apical part of the latter, or towards the central disk, thus forcing the whole rhabdosome to grow backward, so to say, towards the center of the colony. Wiman's figure of the initial part of the rhabdosome of Climacograptus and Gurley's figure of a colony indicate a mode of growth similar to the one described, only that in Climacograptus the colony apparently consisted of only one (the primary?) rhabdosome, as perhaps all siculæ became detached and developed colonies of their own. Also in Monograptus the same mode of growth prevailed. In Phyllograptus the rhabdosome grows also in an opposite direction to the sicula, but no virgula has been found by Holm, and the mode of fixation of the rhabdosome is still doubtful.

In the other genera of the Graptoloidea, however, it has been found that the first theca grows more or less in the direction of the sicula. As a result, the sicula remains near the central disk, at the proximal end of the rhabdosome, and the latter grows distally. In the Dichograptidæ the whole colony is formed by dichotomous branching from one sicula, which remains at the center of the colony.

With the two different directions of growth of the rhabdosomes from the siculæ the presence of a virgula as rod in the rhabdosome is closely connected; for, by the observations of Tullberg, Törnquist, and Holm, the fact has been established that only the Graptoloidea with inward-growing rhabdosomes (Diplograptidæ, Monograptus) have virgulæ, while the others have none. The explanation of this is found in the observation that the initial part of the sicula of probably all Graptoloidea is prolonged into a process (the virgula of Wiman, the hydrocaulus of Ruedemann, the nema of Lapworth), and that this process in the inward-growing rhabdosomes becomes incorporated as virgula, while in the outward-growing rhabdosomes it remains outside (the nemacaulus of Lapworth). The virgula was originally hollow. This is indicated by Wiman's observations in Monograptus and by the growth of gonangia from the central disk in Diplograptus, which gives the hydrocaulus the character of a stolon.

The demonstration that the virgula or "solid axis" of the older authors is present only in a very restricted number of Graptoloidea is of great interest, as the presence of this organ has been considered as one of the principal characters of the graptolites and has even procured them the name "Rhabdophora." The virgula, as identical with the hydrocaulus or nema of the sicula, is, in reality, present in probably all graptolites, for long filiform processes of the sicula have been observed in numerous genera (*e.g.*, Mæandrograptus, Didymograptus, Tetragraptus). Lapworth concludes from the presence of this process that all rhabdosomes were either fastened to a central disk, as in the Dichograptidæ and Diplograptidæ, or directly by the nema to foreign bodies.

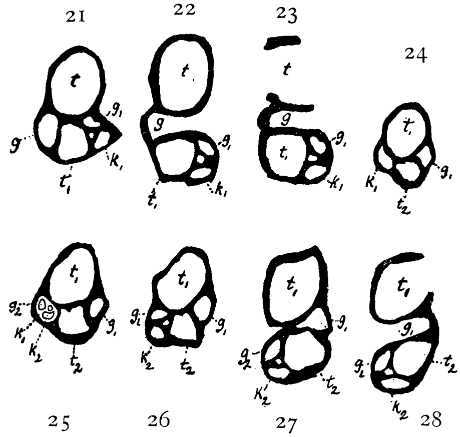
We cannot leave the Graptoloidea without mentioning the important investigations of Tullberg (**'82**), Jækel (**'90**), Perner (**'94**), and Gürich (**'93**, **'96**) on the shape and position of the thecæ, and their apertures in Monograptus, which led to the division of the genus into the two subgenera Pomatograptus Jækel (*Monograpti reversi* Gürich) and Pristiograptus Jækel (*Monograpti erecti*), the interesting study of the phylogeny of the Dichograptidæ by Nicholson and Marr (**'95**), based on the shape of the thecæ, and the work of Miss G. L. Elles (**'97**) on the relations of the subgenera Petalograptus and Cephalograptus.

The knowledge of the structure and development of the rhabdosomes of the Retioloidea is still so uncertain that it can be passed here with the remark that a different number of so-called virgulæ and an "initial canal" of the rhabdosome have been observed.

The most interesting discoveries have apparently been made in regard to the third group of graptolites, the Dendroidea. These finely branching, plant-like graptolites, on account of the absence of a virgula and the occasional presence of a distinct organ of fixation, which indicated a sessile mode of life, in opposition to the generally supposed floating habit of the Graptoloidea and Dendroidea, have been mostly separated from the other graptolites, and are often unhesitatingly united with the campanularians (*cf.* Zittel, '79). Their occurrence only as flattened films prevented, until recently, all attempts at closer investigations. The first indication of a more complicate structure was given by Holm ('90) in his description of *Dictyonema cervicorne.* He found that the branches of the rhabdosome in this species consist of vertical rows of thecæ, which end in hayfork-like spines. Situated alternately on two sides of these spines are peculiar cup-shaped bodies ("by-thecæ"), which he compares to birds' nests and supposes to have been gonangia. While Holm first isolated these delicate fossils from the limestone matrix, Wiman ('95, '96) went further, applied the microtome to them, and obtained a complete series of thin sections of Dictyonema, Dendrograptus (?), and Ptilograptus. The important result of his microscopic analysis is the discovery that the morphological structure of the Dendroidea is much more complex than was suspected, and that there are not less than three different forms of thecæ, *viz.*, thecæ proper, or nourishing individuals, alternating canals (Holm's by-thecæ), which Wiman also considers as gonangia, and gemmating individuals. The following illustrations (Figs. 21–28), selected from a series of one hundred and twenty-five sections through a branch of *Dictyonema rarum* Wiman, show this diversity of the thecæ quite plainly. The nourishing individuals are denoted by *t*, the gonangia by *g*, and the budding individuals by *k*. Fig. 22 shows the opening of the gonangium on the right side; Fig. 23, the ceasing of the theca; Fig. 24, the growth of a new theca. In section 25 the budding individual has produced three new individuals, the further growth of which is shown in section 26, while in section 28 the opening of the next gonangium can be seen.

The hayfork-like outgrowths of the thecæ observed by Holm and Wiman are supposed by the latter to have aided in the process of propagation. In the writer's opinion, they also remind one of the nematocalyces of certain Plumularidæ, which are similar processes provided with a nematophore or altered individual for the purpose of seizing food. They would then constitute a fourth kind of individual.

While it becomes apparent from these discoveries that the three groups of graptolites are more different than had been supposed, it yet seems allowable to retain them in one class. The systematic position of this class seems, by the observed complex structure of the periderm and the high organization of the rhabdosome in general, to have become more uncertain than ever before. As we saw before, the grapolites have, for a long time, quite generally been united with the campanularians. Lately, objections against this union have been raised, especially by Jækel and Neumayr ('89). Wiman holds the same view as Neumayr, namely, that the graptolites cannot be placed in any of the groups of living animals, while Ruedemann sees in the gonangia of Diplograptus a new indication of relationship with the Sertularidæ. Whatever the relations of the grapto-



FIGS. 21–28. — *Dictyonema rarum* Wiman: series of transverse sections (Wiman).

lites may be, it certainly is necessary for the understanding of the life history of the individuals of the colonies to compare the graptolites with some class of living animals, and there is undoubtedly no other class available but the order of Campanulariæ. It also should not be forgotten that the virgula, which always has been considered as constituting one of the principal differences between graptolites and campanularians, has been proved to be comparable to the hydrocaulus of the first theca of the Campanulariæ.

Another difference between graptolites and campanularians has been supposed to consist in the floating habit of the former. This leads us to the interesting question as to the mode of life of the graptolites, which lately has been discussed by an author (Lapworth, '97) whose lifelong study of these fossils, both in the laboratory and in the field, gives his views the greatest moment.

The peculiar mode of occurrence of the graptolites, *viz.*, in numberless multitudes of broken rhabdosomes in highly bituminous shales, which are otherwise poor in fossils, their astonishingly wide horizontal distribution and limited vertical range, has often been an object of speculation. But it is now to be hoped that, by the light shed lately on the structure and development of the colonies, by the exhaustive study of their distribution, and especially also by the researches which recently have been carried on so extensively in regard to the conditions and distribution of life in the ocean, the clue to the understanding of their mode of occurrence will be found. The works of Walther ('93) and Ortmann ('96) have done much to make the results of these bionomic researches known among geologists, and Walther's investigation has given the direct instigation to Lapworth's valuable discussion.

The common consensus of two generations of geologists, says Gurley, has been that the true graptolites (Graptoloidea, Retioloidea) were "floating." Jækel and Wiman, on the other hand, concluded from the heavy chitinous covering of the thecæ and the presence of the virgula as a supporting rod that the rhabdosomes were not suspended, but that the colonies were lightly moored to the ground. Ruedemann ('97) was forced to believe in the sessile mode of life of at least one species of Diplograptus by the finding of a slab (*cf. op. cit.*, Pl. V) which showed a great number of well-preserved colonies spread out regularly in about equal distances from each other and arranged in a well-defined area. Gürich ('**96**) and Lapworth ('**97**) have advanced ideas lately as to the mode of life of the graptolites which correspond to each other, and which apparently explain many of the peculiar features in the distribution of these fossils.

Lapworth found in Great Britain that graptolites may occur in all sediments, but that they are found only in great numbers in rocks containing a considerable amount of carbonaceous matter, and that the frequence of the graptolites is directly proportional to the amount of bitumen present and to the fineness of grain in the matrix. As the least motion in the water would carry away the light carbonaceous matter, Lapworth concludes further that the relative frequency of graptolites in a sediment depends also on the quietude of the water in which the rock was formed. This view is especially interesting to the writer in reference to his observation of a parallel arrangement of the rhabdosomes of graptolites in the Utica shale of the Mohawk Valley ('**97**). This arrangement indicates the passing, during the Utica epoch, of a constant current in a northeast to southwest direction along the southern coast of the Adirondack crystalline area. As the alternation of graptolite-bearing shale and coral-line limestone in the lower part of the Utica shale proves, the current must have been strong enough to bring in the fine mud forming the shale, but cannot have been strong enough in the greater depths, where the deposition took place, to drag the well-preserved, delicate rhabdosomes for a long distance. The occurrence of numerous perfect colonies in two localities is proof of the occasional presence of almost perfect quietude. The latter, however, was the rare exception, the rule having been a slight motion, the traces of which can be found throughout the whole system of shales. The fine sinking mud undoubtedly assisted greatly in keeping the carbonaceous matter at the bottom.

Lapworth further opposes the opinion, so often advanced, that the graptolites furnished the carbonaceous matter in the matrix on the grounds that they are rarely found in a partly decomposed state. From the appearance of the colonies and their fragments, it is concluded that they sank slowly through quiet water to the bottom. As the carbonaceous matter in the rocks is a steady companion of the graptolites, it is supposed to have sunk together with the latter. The source of this carbonaceous matter is found by Lapworth in seaweeds, which, like the living sargassum, were pseudo-planktonic; that is, were originally sessile, but, being torn off, continued to live and were carried by the currents into all seas. Just as the richest fauna of campanularians is still to-day found on the floating seaweeds of the Gulf Stream, so the graptolites are supposed to have flourished on the floating masses of palæozoic algæ. To strengthen this theory, Lapworth calls attention to the fact that it has been found that the rhabdosomes are either fastened to a central disk or have at least a nema. Both central disk and nema indicate that the graptolites were sessile. The Dendroidea alone, which are never so common as the other graptolites, fastened themselves to rocks and stones, and belonged to the "benthos" (lived at the bottom). Originally, however, all graptolites were benthonic, and become only later pseudo-planktonic. This change in the habitat necessitated a change also in the direction of the thecæ, which is indicated in the course taken by the first theca of Diplograptus (Fig. 2), and by the direction of the thecæ of Monograptus and of the branches of Didymograptus, Tetragraptus, and Phyllograptus.

It cannot be denied that the peculiarities of the distribution of the graptolites and their structure are well explained by Gürich's and Lapworth's theories. It is highly probable that many graptolites were indeed pseudo-planktonic, while some may even have gone further and have become free-floating or planktonic, and others are known to have been sessile at the bottom.

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